

Comparative study of walking and climbing speeds among Neotropical harvestmen from Costa Rica

Adam T. Smith, Dayna R. Cook, Megan B. Johnson and Victor R. Townsend, Jr.¹: Department of Biology, Virginia Wesleyan College, 1584 Wesleyan Drive, Norfolk, Virginia 23502, USA

Daniel N. Proud: Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70504-2451, USA

Abstract. Relatively little is known about factors that contribute to microhabitat selection among Central American harvestmen. In this study, we compared walking and climbing speeds for five common species from Costa Rica representing the families Cosmetidae (3 species), Gonyleptidae (1 species) and Sclerosomatidae (1 species). Our sample included two arboreal species, two species that infrequently occupy perches in the vegetation, and one species that rarely climbs. Our analyses revealed no significant interspecific differences in climbing speed, although species with relatively long legs walked significantly faster than species with shorter legs. An arboreal habit did not correlate with increased climbing speed, and all species walked significantly faster than they climbed.

Keywords: Cosmetidae, Gonyleptidae, habitat selection, Opiliones, Sclerosomatidae

The kinematics of terrestrial and arboreal locomotion for members of the order Opiliones are poorly known (Sensenig & Shultz 2007), although individuals of most species of harvestmen generally walk in a manner similar to insects (Shultz & Pinto-da-Rocha 2007). Legs I, III and IV of the harvestman support the body and move in an alternating tripod gait, whereas leg II is used primarily as a tactile sensory organ during walking (Shultz & Pinto-da-Rocha 2007). In climbing, sclerosomatid harvestmen (*Leiobumum* spp.) use the large number of tarsomeres on leg II to form coils that enable individuals to cling to vegetation (Guffey et al. 2000).

Neotropical harvestmen occupy a variety of terrestrial and arboreal habitats including caves, trees, leaf litter, phytotelmata (tree holes and tank bromeliads), palm frond sheaths, rotting logs and cavities beneath rocks (Burns et al. 2007; Curtis & Machado 2007). Individuals may use spaces within vegetation or under rocks or logs as diurnal refugia (Acosta & Machado 2007; Proud et al. 2011). After dusk, however, harvestmen generally forage in the leaf litter and may also climb on vegetation in search of prey or mates (Machado et al. 2000; Willemart & Gnaspini 2004; Wade et al. 2011). Abiotic factors such as temperature and humidity have a major effect upon microhabitat selection and activity patterns (Todd 1949; Edgar 1971). Prior research has suggested a correlation between leg structure and the occupation of arboreal habitats (Curtis & Machado 2007). In Neotropical gonyleptid and temperate sclerosomatid harvestmen, individuals of species that have a greater number of tarsal segments or relatively longer legs tend to occupy higher perches in the understory and on tree trunks than others that possess fewer tarsomeres or shorter legs (Curtis & Machado 2007). Arboreal arachnid species with suspensory locomotion are predicted to benefit from pendulum mechanics and are predicted to possess relatively longer legs that confer greater capabilities than terrestrial species (Moya-Laraño et al. 2008).

Most ecological studies of Neotropical harvestmen are of South American species (Pinto-da-Rocha et al. 2005; Bragnolo et al. 2007). Relatively little is known about the behavior, ecology or natural history of most species of harvestmen from

Central America (Townsend et al. 2010; Townsend et al. 2011; Proud et al. 2012). The wet tropical forest at La Selva Biological Station, Costa Rica, supports a diverse harvestmen fauna including representatives of the families Cosmetidae (19 species), Gonyleptidae (3 species), Sclerosomatidae (6 species), Stygnommatidae (1 species), and Zalmoxidae (7 species), as well as the genus *Costabrimma* (2 species) (Proud et al. 2012). The most common species are *Cynorta marginalis* Banks 1909 (Cosmetidae), which actively climbs trees after dusk, and members of the genus *Prionostemma* (Sclerosomatidae), which frequently form loose aggregations on trees during the day and actively wander through the leaf litter as solitary individuals after dark (Wade et al. 2011). Other relatively common, but generally less abundant, species include the cosmetid harvestmen *Eupoecilaema magnum* Roewer 1933 and *Paecilaema* sp., which infrequently climb the vegetation but are most frequently encountered within palm fronds or decaying logs (Proud et al. 2012). Species representing the families Gonyleptidae, Stygnommatidae and Zalmoxidae inhabit the leaf litter and are rarely observed climbing vegetation (Proud et al. 2012).

The objective of this study was to examine the relationship between field observations of habitat use and locomotion in Costa Rican harvestmen. Specifically, we sought to compare walking and climbing speeds for five species of harvestmen: two highly arboreal (*C. marginalis* and *Prionostemma* sp.), two that are occasionally found on vegetation (*E. magnum* and *Paecilaema* sp.), and one primarily terrestrial species (*Glysterus* sp.). We predicted that the arboreal species would climb significantly faster than terrestrial species. Based upon general observations of the importance of relative leg length (reviewed by Curtis & Machado 2007), we also predicted that species with relatively longer legs (*Prionostemma* sp. and *E. magnum*) would walk and climb significantly faster than species with shorter legs (*C. marginalis* and *Glysterus* sp.).

METHODS

Our study was conducted at La Selva Biological Field Station (10°26'15.03"N, 84°00'1.19"W, datum: WGS84) from 6–19 July 2010. We captured harvestmen by hand opportunistically between 1200–1600 h from palm frond sheaths, tree trunks and leaf litter. Prior to testing, individuals were

¹ Corresponding author. E-mail: vtownsend@vwc.edu

communally housed in mesh cylindrical containers (height = 23 cm, diameter = 14 cm) with damp paper towels. Small branches and leaf litter were added to the containers to provide structure and hiding places. Harvestmen were kept in a shade tent at ambient temperatures (25–30 °C) for 24–48 h prior to testing and were given fresh tropical fruit and water ad libitum.

We conducted trials from 1900–0100 h under red light to minimize disturbance of individuals (Hoenen & Gnaspini 1999). Trials were randomized with respect to type (walking or climbing), species and individual. To control for the impact of leg autotomy (a defense mechanism employed by *Prionostemma*, but not by the other species in our study; Gnaspini & Hara 2007) in both experiments, we only used adult harvestmen that had all eight legs ($n = 30$ individuals per species for all species except *Glysterus* sp., for which $n = 24$). The speed (cm/s) of each harvestman was measured once for walking and once for climbing in random sequence.

To determine a walking speed, we constructed a horizontal track (70 cm length \times 8 cm wide) using four meter sticks. On each side of the track, the first meter stick was placed flat and a second was positioned on its side on top of the first, enabling us to easily read cm increments while providing enough clearance (3.5 cm) for even the largest individuals. The floor of the trackway was lined with moistened paper towels. To prevent harvestmen from escaping, we placed thin sections of plexiglass over the top of the trackway. Similar to the protocol employed by Guffey (1999), we held each harvestman by legs III and IV at the 0 cm mark at the beginning of each trial until it was motionless. After gently releasing it, we measured the time that it took to walk to the 70 cm mark. In many trials, the harvestmen paused or ceased moving and then resumed walking. To determine speed while moving, we stopped timing during such pauses.

To determine the climbing velocity of each individual, we used a large, vertically suspended leaf (approximately 80 cm in length) that was freshly cut from a split-leaf palm (*Geonoma cuneata*) as a test surface. Each night we used a new, freshly cut leaf. We marked each leaf with 10 cm increments to a final mark of 70 cm and suspended it in the vertical position. We used the same protocol for handling and observing harvestmen as in the walking experiment. After measuring walking and climbing speeds, we preserved individuals in 70% ethanol.

The residuals for the walking data were not normally distributed (Shapiro-Wilk test: $W = 0.891$, $P < 0.001$). Residuals for climbing velocities likewise did not meet the assumptions of normality (Shapiro-Wilk test: $W = 0.925$, $P < 0.001$). Therefore we applied a $\log(x+1)$ transformation to the data. Log transformed walking speeds met the assumptions of normality (Shapiro-Wilk test: $W = 0.984$, $P = 0.08$) and homogeneity (Bartlett test: $K^2 = 2.128$, $df = 4$, $P = 0.712$). Log transformed climbing speeds also met the assumptions of normality (Shapiro-Wilk test: $W = 0.986$, $P = 0.248$) and homogeneity (Bartlett test: $K^2 = 4.455$, $df = 4$, $P = 0.348$).

In order to test for interspecific differences in walking or climbing speeds, we employed two separate single factor ANOVAs. Because we used the same individuals for both walking and climbing, we used a Bonferroni correction to calculate an adjusted alpha level ($\alpha = 0.025$). For significant differences detected by the ANOVA, we applied a post-hoc

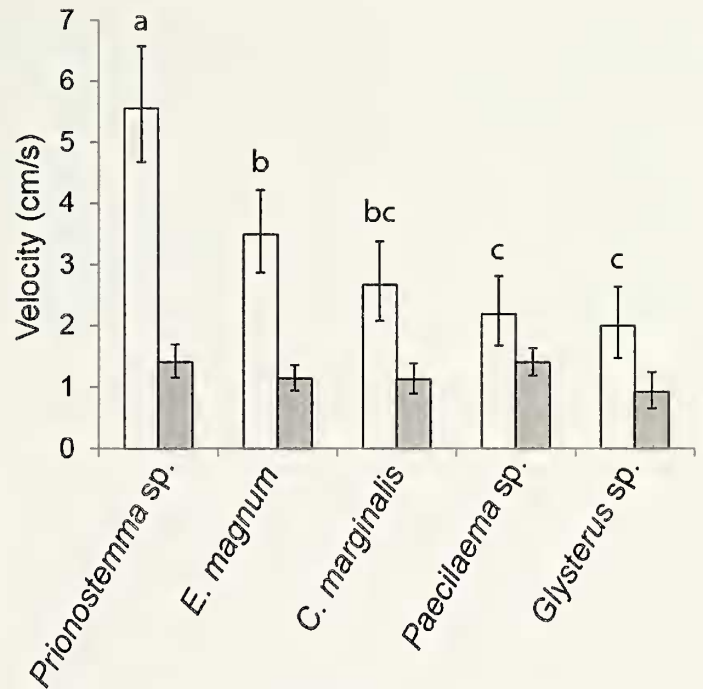


Figure 1.—Mean walking (white bars) and climbing (gray bars) speeds with 95% CI for five species of harvestmen. Significant differences among species are indicated with different letters.

Tukey Honest Significant Differences method to determine which species differed. Additionally, to test the hypothesis that walking and climbing rates are correlated for each of the five species we utilized pairwise Mann-Whitney U tests ($\alpha = 0.05$). Means and 95% confidence intervals for walking and climbing speeds (cm/s) were calculated from log-transformed data and back-transformed (Fig. 1).

In the species of harvestmen examined in our study, legs III and IV are important in terrestrial locomotion, similar in relative length, and both are significantly longer than leg I. We used the mean length of leg IV to test for correlations between walking speed and leg morphology. Using digital calipers, we measured the total length of leg IV (mm) for all specimens tested. Despite multiple attempts to transform the data, the residuals for the leg length data were not normally distributed, and variances were not homogeneous. Therefore, we analyzed these morphometric data using Kruskal-Wallis rank sum tests followed by Mann-Whitney U tests to test the null hypothesis that leg IV length does not differ between species. We report means and standard deviation as a measure of central tendency since mean values did not differ greatly from the medians, and because other data are expressed as means.

We calculated species means from log transformed data for leg length, walking speed and climbing speed, back-transformed the means and 95% CI, and employed regression analyses to determine if mean leg length affected mean walking and climbing speeds. We used means because leg length data were not collected at the time of walking and climbing trials, and thus leg length measurements were not paired with time trials for each individual. We tested the null hypotheses that there is no relationship between leg length and walking or climbing speed (the slopes of the regression lines equaled zero). This provided a preliminary basis for assessing the effects of leg

Table 1.—Ecological and morphological comparisons of Costa Rican harvestmen examined in this study. For climbing status, species are classified as arboreal (A), semi-arboreal (S), or rarely arboreal (R). General habitat preferences are provided for day (D) and night (N) and are based upon the field data presented by Wade et al. (2011) and Proud et al. (2012). For morphological characteristics, we calculated the mean \pm SD for scutal length and for the length of leg IV. Samples sizes are $n = 24$ for *Glysterus* sp., and $n = 30$ for each of the other four species.

Species	Climb status	Habitat preferences	Scutal length (mm)	Length of leg IV (mm)
<i>C. marginalis</i>	A	Terrestrial (D, N) Arboreal (D, N)	4.2 \pm 0.4	38.0 \pm 6.6
<i>E. magnum</i>	S	Terrestrial (D, N) Arboreal (N)	6.8 \pm 0.5	57.4 \pm 7.6
<i>Paecilaema</i> sp.	S	Terrestrial (D, N) Arboreal (N)	4.9 \pm 0.3	30.4 \pm 2.4
<i>Glysterus</i> sp.	R	Terrestrial (D, N)	5.0 \pm 0.4	14.7 \pm 1.8
<i>Prionostemma</i> sp.	A	Arboreal (D) Terrestrial (N)	4.6 \pm 0.8	66.7 \pm 6.1

length on walking and climbing speeds for these species. All statistical analyses were implemented in R (R Development Core Team 2010).

RESULTS

Walking speed differed significantly among species ($F = 13.69$, $df = 4$, $P < 0.001$); however, no significant differences were detected for climbing speeds ($F = 1.97$, $df = 4$, $P = 0.105$). The pairwise post-hoc comparisons indicated that the mean walking speed of *Prionostemma* sp. was significantly faster than all other species (Fig. 1). Additionally, *E. magnum* walked significantly faster than *Paecilaema* sp. and *Glysterus* sp., but no differences were detected in walking speed between *Paecilaema* sp., *C. marginalis* and *Glysterus* sp. (Fig. 1). Results of the Mann-Whitney U tests revealed that all species walked significantly faster than they climbed (Fig. 1; all $df = 1$, *Prionostemma*: $U = 40.4$, $P < 0.001$; *E. magnum*: $U = 27.5$, $P < 0.001$; *Paecilaema*: $U = 19.5$, $P < 0.001$; *C. marginalis*: $U = 5.39$, $P = 0.02$; *Glysterus*: $U = 7.01$, $P = 0.008$).

Relative leg length (Table 1) differed significantly among species (Kruskal-Wallis $\chi^2 = 133.7$, $df = 4$, $P < 0.001$).

Prionostemma sp. had the longest leg length followed by *E. magnum*, *C. marginalis* and *Paecilaema* sp., respectively. *Glysterus* sp. had the shortest leg length.

We rejected the null hypothesis that the slope of the line $\beta_1 = 0$ for the regression of mean walking speed against mean leg length: $r^2 = 0.771$, $df = 3$, $P = 0.032$, regression equation $y = 0.569 + 0.635x$, where $y =$ walking speed (cm/s) and $x =$ length of leg IV (cm) (Fig. 2A). Mean leg length had no significant effect on mean climbing speed, and we were not able to reject the null hypothesis that $\beta_1 = 0$: $r^2 = 0.10$, $df = 3$, $P = 0.32$, regression equation $y = 0.965 + 0.056x$, where $y =$ climbing speed (cm/s) and $x =$ length of leg IV (cm) (Fig. 2B).

DISCUSSION

There are relatively few published walking or climbing speeds for harvestmen (Houghton et al. 2011). Schmitz (2005) examined the impact of movement upon metabolic rate using running velocities up to 96 cm/min for two species. Guffey (1999) and Houghton et al. (2011) assessed the impact of leg autotomy upon walking speeds for sclerosomatid species and reported velocities up to 9.3 cm/s for individuals with all eight

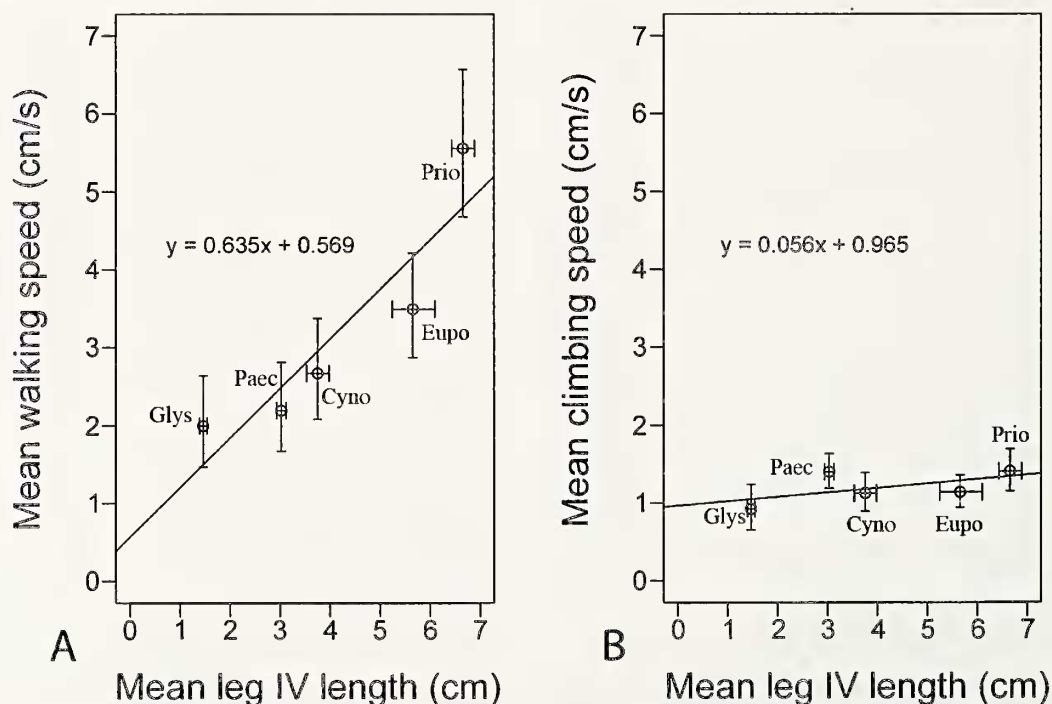


Figure 2.—Regression of mean leg IV length on speed with 95% CI for five species of harvestmen. A) Mean walking speed as a function of mean leg IV length. B) Mean climbing speed as a function of mean leg length. Abbreviations: Glyc = *Glysterus* sp.; Paec = *Paecilaema* sp.; Cyno = *Cynorta marginalis*; Eupo = *Eupoecilaema magnum*; Prio = *Prionostemma* sp.

legs intact on a flat, horizontal surface. Our data indicate that species with relatively longer legs walk significantly faster than species with shorter legs, but that climbing speed is not affected by leg length. The mean lengths for leg IV of *Prionostemma* sp. and *E. magnum* exceed 55 mm, whereas those for *C. marginalis*, *Paecilaema* sp. and *Glysterus* sp. are much shorter.

Our results also indicate that harvestmen walk significantly faster than they climb, regardless of the habitat in which they are most frequently encountered. In addition, climbing speed did not significantly vary between species, regardless of relative leg length. Curtis and Machado (2007) cautiously reported a functional relationship between leg morphology and the use of arboreal habitats for sclerosomatid harvestmen. In our study, the arboreal *C. marginalis* (short legs) and *Prionostemma* (long legs) sp. climbed at speeds that were not significantly different from each other or from that of the leaf litter residing *Glysterus* (short legs).

In our study, the most arboreal species use the surfaces of trees in different ways. During the day, adult *C. marginalis* occupying perches on trunks or buttresses are inactive (Wade et al. 2011). However, after dusk they become active and climb, interact with conspecifics and forage (Wade et al. 2011). In contrast, adult and nymphs of *Prionostemma* sp. assemble in loose aggregations on arboreal perches during the day and descend to the leaf litter after dusk, presumably to forage (Wade et al. 2011).

Interspecific variation in walking speeds may reflect different strategies for life in the leaf litter microhabitat. Individuals of *Prionostemma* sp., the most vagile species in our sample, are capable of moving considerable distances (up to 0.2 km/night) in forested habitats (Donaldson & Grether 2007, Grether & Donaldson 2007). These harvestmen may rely in part upon fast walking speeds to elude potential invertebrate and vertebrate predators (Gnaspini & Hara 2007). Shorter-legged, less vagile species such as *C. marginalis*, *Paecilaema* sp., and *Glysterus* sp. may use slow movement to avoid detection by visually oriented predators (Gnaspini & Hara 2007). More detailed natural history studies of each of these species are required to assess these hypotheses.

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